Richness of bryophyte vegetation in near-natural and managed beech stands: the effects of management-induced differences in dead wood

Péter Ódor and Tibor Standovár

In order to explore the importance of near-natural beech forest in maintaining the diversity of bryophytes, a near-natural montane beech stand was compared with five neighbouring managed stands of different ages in northern Hungary. Bryophyte vegetation on dead wood and volcanic rock outcrops was studied. Species richness, abundance, different diversity measures and the importance of dead wood in bryophyte diversity were analysed.

Analyses are based on presence/absence data of bryophytes collected in 50 × 50 m sample plots in which blocks of 100 cm² microplots were systematically distributed. Altogether 34 bryophytes occurred in this sample. Amount and quality of dead wood was estimated by using line intercept sampling.

Bryophyte vegetation was richer in the near-natural stand, especially in the moist rocky site. Species richness, abundance, Shannon-Wiener diversity and evenness as well as diversity of realized species combinations were much higher than in any managed plot. This site also contained the largest amount and variation (tree species, size, decay phase) of dead wood. Bryophyte vegetation of the managed plots was much scarcer and much less diverse. These plots tended to contain very little dead wood of small size and early decay classes. The only exception was a recently thinned stand where the presence of fine woody debris supported a relatively high number of bryophytes including a few species inhabiting dead wood.

It is argued, that successful maintenance of bryophyte diversity in central European beech forests requires not only the preservation of the small isolated near-natural stands, but also a reasonable dead wood management in the matrix of commercial forests. Large and hence long lasting logs are inevitable in providing appropriate establishment sites for the most sensitive hepatics that are rare habitat specialists with limited dispersal capacity.

P. Ódor (odor@ramet.elte.hu) and T. Standovár, Dept of Plant Taxonomy and Ecology, L. Eötvös Univ., Ludovika tér 2., H-1083 Budapest, Hungary.
tion has strong effects on the composition and structure of both juvenile trees and herbaceous species mainly because of the resulting changes in light availability (Horn 1976, Woods and Whittaker 1981, Canham and Marks 1985, Collins et al. 1985, Peterken 1996, Emborg 1998). Besides heterogeneity of light conditions, natural dynamics also results in accumulation of dead organic material on the forest floor (Falinski 1978, Peterken 1996, Kirby et al. 1997). Dead wood plays an important role in forest ecosystem processes as nutrient storage. It also provides habitat and food for many dead wood dwelling organisms including fungi, beetles, birds and mammals (see references in Harmon et al. 1986, Peterken 1996).

Modern silviculture reduces the natural amount of dead wood found in both deciduous (Kirby et al. 1997) and boreal forests (Kruys et al. 1999). In the boreal zone studies on dead wood quality showed that the proportion of fine woody debris is much higher in managed stands (Kruys and Jonsson 1999). Large logs are extremely rare, coarse woody debris is mostly represented by stumps, and later decay stages are scarce in managed stands (Söderström 1988b, Kruys et al. 1999).

Large logs can support rich bryophyte vegetation. Several mosses and liverworts occur preferentially or exclusively on decaying logs (Söderström 1993, McAlister 1997), and specific bryophyte communities were also described (Philippi 1965, Fehér and Orbán 1981). Since dead wood is a continuously changing and temporary habitat, the composition and structure of bryophyte assemblages also changes with time. Succession in spruce forest starts with epiphytic species, later epixylous, then soil inhabiting species dominate (McCullough 1948, Muhle and LeBlanc 1975, Söderström 1988a). In deciduous beech and oak forests the soil surface is covered by a thick litter layer, which inhibits the development of a mossy cover, consequently the main habitats for bryophytes are rocky outcrops, decaying wood and bark. The forest floor is only inhabited after soil disturbance (e.g. uprooting), and then mostly by colonist species (Jonsson 1993).

Dead wood accumulation is rare in European forests, since most of these are being managed intensively. Consequently, populations of bryophytes inhabiting dead wood are threatened. Fragmentation and destruction of near-natural forests threaten those bryophytes that are restricted to such forests, and have limited dispersal capacity, thus occur in small isolated populations (Söderström 1990). Of the 566 bryophyte species that have been described from Hungary, 62 species occur on dead wood, of which 37 (mostly liverworts) can be treated as regionally rare (on the basis of Orbán and Vajda 1985).

In a previous study (Ódor and Standovár unpubl.), bryophyte vegetation was studied in a near-natural montane beech stand in northern Hungary. Substrate specificity, interspecific relationships and species combinations were studied. Analyses of species-substrate associations showed that most species exhibit substrate preference. Species characteristic of bare rocks, humus rich outcrops and coarse woody debris (CWD) were distinguished. Bare rocks are inhabited by distinct assemblages of only a few species, whereas the bryophyte vegetation of humus rich outcrops contains several species also characteristic of CWD. This means that the presence of CWD, not only provides habitat for wood inhabiting bryophytes, but also resulted in diverse rupicolous bryophyte assemblages on humus rich outcrops.

The aims of this study were the following: 1) to compare the bryophyte vegetation of the studied near-natural beech stand with that of neighbouring managed stands (representing all available age classes) on similar sites. 2) To compare the amount, size and decay status of dead wood in these beech stands. 3) To demonstrate the importance of dead wood in maintaining the diversity of bryophyte vegetation in these beech stands.

Materials and methods

Study area

The study was carried out in the Kékes Forest Reserve and in five surrounding managed stands (Fig. 1). Kékes, in the Mátra Mts, is the highest point in Hungary (1014 m). Climate is relatively continental with 5.7°C mean annual temperature, low winter (–4.7°C in January) and high summer temperatures (15.5°C in July). Precipitation is ca 840 mm of which 480 mm falls during the growing season. The bedrock is andesite and the topography is extremely steep, scree slopes being characteristic. The shallow brown forest soils are mainly covered by montane beech wood (Aconito-Fagetum Soó). Mixed maple-ash-lime woodland (Phyllitidi-Aceretum subarcapaticum Soó) occurs in the most humid and rocky patches of the reserve (Kovács 1968). Bryophyte vegetation belongs to the Paraleucobyrtetum longifolii Sjögren synusia on andesite rocks (Sjögren 1964, Hübschmann 1986); and to the Blepharostomion trichophylli Barkmann synusia on decaying wood (Barkmann 1958, Hübschmann 1986). Ódor (2000) gave a thorough qualitative description of the bryophyte flora and vegetation of the reserve.

The Kékes Forest Reserve (63 ha) is one of the last vestiges of near-natural Central-European montane beech woods in Hungary. The stand is a mosaic of different forest developmental phases, with trees older than 200 yr occurring together with many younger age classes. It is also a mosaic of two community types, which differ in stand structure. Large trees that form a closed canopy with a few small gaps dominate montane beech wood patches (SOIL habitat type). In contrast, in mixed maple-ash-lime patches (SCREE habitat type) large canopy trees are virtually missing in many parts, since large gaps with many large fallen logs predominate. The amount of rocks is much higher in this site than in the other parts of the reserve. It is
assumed that regeneration is slower, and gaps are larger because of extreme site conditions. Species composition indicates ravine-like habitats with high humidity.

The understorey layer is scarce, consisting mostly of advanced regeneration of beech and *Daphne mezereum*. *Sambucus racemosa* and *Ulmus glabra* grow on scree sites. In the ground layer, *Galium odoratum*, *Mercurialis perennis*, *Dentaria bulbifera*, *Viola sylvestris* and *Oxalis acetosella* are the most frequent vascular species, together with seedlings of *Fagus sylvatica* and *Acer pseudoplatanus*. In the scree sites *Urtica dioica*, *Impatiens noli-tangere*, *Solanum dulcamara* and *Athyrium filix-femina* are the dominant species. Accumulations of coarse woody debris (CWD) are characteristic of this near-natural stand, which, along with rocky outcrops, accounts for a rich epixylous bryophyte vegetation.

All the five managed stands, chosen for comparisons, have as similar topography as possible (northeasterly aspect, similar steepness) to that of the Kékes Reserve (26F), though they are situated a bit lower elevation – between 600 and 800 m a. s. l. (Fig. 1). Gálhidy (1999) described the stand structure in all investigated stands. All of them are almost pure beech stands. The youngest stand (26D) is ca 25 yr old, mean diameter at breast height (DBH) is 10.1 cm. This stand is now part of the reserve that was created after this part had been clear-cut, but it means that no thinning and tending cuts have been done recently. Site conditions are similar to those in the SOIL habitat type of the old-growth stand. There are two ca 40-yr-old stands. One of them (31B) was thinned in 1997 (mean DBH is 18.6 cm), whereas the other (29D) has not been thinned recently (mean DBH is 11.8 cm). Older managed forests are represented by two 80–90-yr-old stands (34C, 36D). Mean DBH was 28.7 cm and 31.1 cm, respectively. The amount of stones in the forest floor is similar in the five managed stands and in the SOIL habitat type in the reserve – mean stone cover is ca 10%. However, the SCREE habitat type differs from them in having much more stones on the surface (mean cover ca 40%), often in larger pieces. The amount of ground layer herbaceous vegetation differs greatly in different stands. In the unmanaged reserve with natural openings and heterogeneous stand structure, mean cover of vascular species is 40% in the SCREE habitat type, and 20% in the SOIL habitat type. Ground layer vegetation is extremely scarce (mean cover < 1%) in all the managed plots as a result of dense, homogeneous canopy structure.
Data collection

In the reserve, a 120 × 120 m plot with heterogeneous stand structure was studied. Vegetation was systematically sampled in 0.5 × 0.5 m quadrats that were set out on a grid at 5 m intervals. Presence/absence data of bryophytes and the type of substrate were recorded in nine systematically distributed circular microplots of 100 cm² in all quadrats. Altogether 5184 microplots were sampled in 576 quadrats. Quadrats were grouped into two habitat types (SCREE and SOIL) based on multivariate numerical classification using slope, aspect and substrate type (percent cover of soil, rock and dead wood) as variables. Managed stands were sampled in the same way, but only 50 × 50 m plots were used. For this reason, two subsamples (50 × 50 m plot, 121 quadrats, 1089 circular plots) of the reserve data were used for the comparison. RES-A represents the SCREE, whereas RES-B the SOIL habitat (Fig. 2, Table 1).

Line intercept sampling was applied to estimate the amount of dead wood, using three 60-m transects in each stand (Warren and Olsen 1964, Van Wagner 1968). Diameter of intercepted logs were measured, decay stage was determined by using an eight-class system modified from McCullough (1948), Söderström (1988a) and Hofgaard (1993): 1) bark intact, appearing live; small branches remaining; wood hard. 2) Bark appearing dead, broken up in patches but >50 % remaining; small branches absent; wood hard. 3) Bark <50 % remaining or absent; wood hard; shape circular. 4) Bark absent; wood started to soften, sapwood (2–4 cm) soft; surface smooth or small crevices present; shape circular. 5) Wood soft; crevices present, small pieces lost; shape elliptic; outline of the trunk intact. 6) Wood soft; wood fragments lost; shape flat elliptic; outline of the trunk deformed. 7) Wood soft, only few wood fragments are present; outline hard to define, trunk is partly hidden. 8) Wood completely soft, pulverised; outline indeterminable, trunk hidden.


Data analyses

The comparison of bryophyte vegetation of the studied plots was based on species composition. Dominance structure was characterised by rank-relative frequency curves. Species diversity and evenness were calculated by using the Shannon-Wiener formula. Calculations were performed by the NUCOSA program package (Tóthmérész 1993, 1996).

Compositional variation of bryophyte community was investigated by analysing realised species combinations (florula), i.e., the different types of species coalitions found in 100 cm² plots. Florula diversity (eq. 1) and florula evenness (eq. 2) are Shannon-type diversity measures, which describe the diversity and evenness of realized species combinations based on their relative frequency.

\[
mH = m \log m - \sum_{k=1}^{\omega} f_k \log f_k \tag{1}
\]

\[
\frac{H}{H_{\max}} = 1 - \left( \sum_{k=1}^{\omega} f_k \log f_k / m \log m \right), \tag{2}
\]

where \(f_k\) = frequency of \(k^{th}\) species combination; \(m\) = sample size; and \(\omega\) = number of realized species combinations.


Calculations were performed by the SYN-TAX program package (Podani 1993).

Results

Altogether 34 species were found in the samples taken in the studied stands. Table 1 shows some basic features of the bryophyte vegetation. The first column shows data for the whole reserve to emphasize the richness of RES-A. More than one third of bryophyte-containing microplots occurs within the fifth of sampling units constituting RES-A and almost the whole species pool (both epixyl and rupicol species pool) is concentrated within this area. The number of microplots containing bryophytes is much higher in both
reserve plots than in the managed ones. Species richness is higher in the reserve than in the managed stands. The only exception is 31B, where the number of species is relatively high. It is caused by the presence of finer woody debris after thinning. Mean species number/microplot is also the highest in RES-A. Shannon-Wiener diversity is highest in the reserve. Both florula diversity and evenness are higher in the reserve plots than in the plots in the managed stands, especially in RES-A. In this plot more species combinations occur (using this sampling unit size) and their frequency distribution is more even.

Rank-relative frequency curves (Fig. 3) show that RES-A is the richest one in subdominants. Dead wood inhabiting species are well represented among these subdominants. Managed stands are characterised by steeper curves. Dead wood inhabiting species are fewer and have lower frequency. RES-B is characterised by more subdominants than in managed plots, but less than that of RES-A. There are only a few dead wood inhabiting species; most of them are rare.

Table 2 shows detailed data on the frequency of species in different plots. Many rare, dead wood inhabiting species are restricted to RES-A. Examples are *Calypogeia suecica*, *Novellia curvifolia*, *Sanionia uncinata* and *Blepharostoma trichophyllum*. There are quite a few subdominant and subordinate species in both reserve plots. In the managed stands the frequencies of species characteristic of humus rich outcrops like *Dicranum scoparium*, *Metzgeria furcata*, *Plagiochila porelloides*, *Homalothecium philippeanum*, *Homalia trichomanoides* and decaying wood (*Lophocolea heterophylla*, *Bryum flaccidum*, *Brachythecium rutabulum*) are low. Combined species richness of all managed plots (20 species distributed in 1.25 ha) exceeds that of RES-B (14 species in 0.25 ha), whereas RES-A alone is much richer in species than the whole range of managed plots.

These differences in bryophyte vegetation could be partly explained by differences in the amount and quality of coarse woody debris in the plots. Figure 4 shows the
estimated amount of coarse woody debris of different diameter classes in the plots. RES-A contains the highest amount of dead wood, and also the highest proportion of thick (>30 cm) logs. The thinned plot (31B) also contains considerable amount, but compared with RES-A and RES-B, the diameter of logs is smaller.

Figure 5 shows the distribution of decay phases. The proportion of well-decayed logs (category > 5) is much higher in the reserve plots than in the managed stands.

Discussion

Comparison of bryophytes in managed and unmanaged stands

The results indicate that bryophyte vegetation is poorer in the managed stands (for all ages) than in the near-natural reserve. Even when data are combined for all age classes, both species richness and overall abundance are much lower. Bryophytes inhabiting dead wood are almost absent from these managed stands. Bryophyte vegetation almost exclusively contains the most common species of rocky outcrops (Grimmia hartmanii, Isothecium alopecuroides, Pterigynandrum filiforme, Paraleucobryum longifolium, Hypnum cupressiforme).

Bryophyte vegetation is most abundant and richest in the SCREE habitat. This richness is attributed to the large amount and variation (species, size, decay phase) of dead wood. The accumulation of organic matter is reflected not only in the richness of log-inhabiting bryophytes, but also in the occurrence of more diverse and more complex rupicolous assemblages. This habitat serves as refugium for some rare species living on logs (Lophozia adscendens and Anastrophyllum bellerianum) (found in the SCREE plot, but not represented in the sample), Nowellia curvifolia, Calypogea succea, Blepharostoma trichophyllum, Sanionia uncinata) and also on outcrops (Tritomaria quinquedentata, Homalia

Table 2. Frequency data (number of occurrences in microplots) for bryophyte species in the studied plots. Substrate preference data are based on Ódor and Standovár (unpubl.): DW-dead wood; LT-living tree (bark); R-rock; S-soil.

<table>
<thead>
<tr>
<th>Species</th>
<th>RESERVE</th>
<th>SUBSTRAT</th>
<th>RES-A</th>
<th>RES-B</th>
<th>26D</th>
<th>31B</th>
<th>29D</th>
<th>34C</th>
<th>36D</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lophocolea heterophylla</td>
<td>116</td>
<td>DW</td>
<td>77</td>
<td>9</td>
<td>1</td>
<td>6</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Bryum flaccidum</td>
<td>76</td>
<td>DW</td>
<td>58</td>
<td>4</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Amblystegium serpen and</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Brachythecium velutinum</td>
<td>66</td>
<td>DW</td>
<td>37</td>
<td>4</td>
<td>0</td>
<td>1</td>
<td>3</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Brachythecium rutabulum</td>
<td>42</td>
<td>DW</td>
<td>34</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Pseudeleskeaella nervosa</td>
<td>13</td>
<td>DW</td>
<td>13</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Blepharostoma trichophyllum</td>
<td>6</td>
<td>DW</td>
<td>5</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Sanionia uncinata</td>
<td>4</td>
<td>DW</td>
<td>4</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Nowellia curvifolia</td>
<td>2</td>
<td>DW</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Calypogea succea</td>
<td>1</td>
<td>DW</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Grimmia hartmanii</td>
<td>747</td>
<td>R</td>
<td>239</td>
<td>75</td>
<td>42</td>
<td>36</td>
<td>31</td>
<td>48</td>
<td>8</td>
</tr>
<tr>
<td>Paraleucobryum longifolium</td>
<td>470</td>
<td>R</td>
<td>120</td>
<td>42</td>
<td>17</td>
<td>3</td>
<td>20</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Isothecium alopecuroides</td>
<td>290</td>
<td>R</td>
<td>144</td>
<td>21</td>
<td>14</td>
<td>8</td>
<td>6</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>Plagiocoma porelloiides</td>
<td>155</td>
<td>R</td>
<td>111</td>
<td>7</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Dicranum scoparium</td>
<td>158</td>
<td>R</td>
<td>109</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Metzgeria furcata</td>
<td>100</td>
<td>R</td>
<td>44</td>
<td>11</td>
<td>2</td>
<td>1</td>
<td>3</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>Homalotheecium philippeanum</td>
<td>37</td>
<td>R</td>
<td>34</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Brachythecium populorum</td>
<td>48</td>
<td>R</td>
<td>15</td>
<td>9</td>
<td>6</td>
<td>6</td>
<td>1</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>Holmaia trichomanoides</td>
<td>19</td>
<td>R</td>
<td>12</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Anomodon viticulosus</td>
<td>1</td>
<td>R</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Cynodontium polycarpon</td>
<td>2</td>
<td>R</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Plagiommia cuspidatulm</td>
<td>1</td>
<td>R</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Hedwiga ciliata</td>
<td>1</td>
<td>R</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>Schistidium apocarpum</td>
<td>0</td>
<td>R</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Hypnum cupressiforme</td>
<td>672</td>
<td>DW</td>
<td>369</td>
<td>47</td>
<td>20</td>
<td>4</td>
<td>0</td>
<td>2</td>
<td>9</td>
</tr>
<tr>
<td>Pterigynandrum filiforme</td>
<td>126</td>
<td>R,LT</td>
<td>28</td>
<td>17</td>
<td>0</td>
<td>7</td>
<td>2</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td>Plagiothecium spp.</td>
<td>107</td>
<td>R,DW,LT,S</td>
<td>58</td>
<td>3</td>
<td>5</td>
<td>6</td>
<td>0</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Plagioiymium ellipticum</td>
<td>20</td>
<td>R,DW,S</td>
<td>18</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Rhizomnium punctatum</td>
<td>27</td>
<td>R,DW,S</td>
<td>15</td>
<td>0</td>
<td>0</td>
<td>6</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Euryhynchium striatum</td>
<td>7</td>
<td>R,DW</td>
<td>6</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Brachythecium salebrosum</td>
<td>6</td>
<td>R,DW,LT,S</td>
<td>5</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Pohlia nutans</td>
<td>8</td>
<td>R,DW,LT,S</td>
<td>3</td>
<td>4</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>Dicranella heteromorallla</td>
<td>5</td>
<td>R,DW,LT,S</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Polytrichum formosum</td>
<td>6</td>
<td>S</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
trichomanoides). Some of these hepatics are restricted to this moist site. They are more sensitive to the decrease in air humidity than several other mosses or lichens (Clausen 1964, Forman 1964). Wood inhabiting bryophyte assemblages are poorer in the SOIL habitat, because the amount of dead wood is lower and the microclimate is less humid than in SCREE. However, rupicole bryophyte vegetation is more abundant and diverse in both SCREE and SOIL than in the studied managed stands.

Based on our results, it is clear that the amount and quality of dead wood are major determinants of bryophyte diversity. However, other factors could also be important. Both the amount and size variation of rocks are much higher in the SCREE habitat, resulting a higher diversity of microhabitats. This habitat diversity and accumulations of decaying woody material among rocks, account for the biodiversity of rupicol bryophyte assemblages (Ódor and Standovár unpubl.).

Admixing trees have their major effects on bark inhabiting bryophytes. Differences among host tree species are less pronounced in late decaying phases. The epixyl bryophytes, restricted to this site, occur exclusively on well-decayed logs. The thinned plot (31B) contained twice as much dead wood as the SOIL habitat type (RES-B) in the reserve (Fig. 4). However, the diversity of bryophyte vegetation is higher in the unmanaged plot. This is more pronounced in the abundance (number of species in microplots, number of non-empty microplots) and heterogeneity (number of species combinations, florula diversity, florula evenness) of the vegetation than in species richness (Table 1). The higher proportion of large logs, the longer continuity of the stand and the vicinity of the diverse SCREE site could contribute to these differences.

In conclusion, bryophyte vegetation is poorer (regarding all vegetation characteristics) in forests (several age-classes) managed for timber production than in near-natural stands. The most important reasons for this include the lower total amount and variation of dead wood and the absence of large logs in managed stands.

All these results are in good agreement with the findings of comparative studies of managed and unmanaged boreal forests (Söderström 1988b, Gustafsson and Hallingbäck 1988, Lesica et al. 1991, Ohlson et al. 1997). The greatest difference was found in the diversity and abundance of dead wood inhabiting hepatics. Their occurrence is restricted to the habitats provided by large logs of intermediate to late decay phase, which are uncommon in managed stands (Söderström 1988b, Kruys et al. 1999). This demonstrates the importance of large decaying logs in maintaining rich bryophyte assemblages. Another important process in unmanaged forests is uprooting which creates new surfaces that are suitable for several colonist species (Jonsson and Esseen 1990).
Considerations for conservation management of dead wood

In temperate deciduous forests the potential habitats for bryophyte patches are more limited than in boreal forests. The thick litter layer prevents the development of soil inhabiting bryophyte assemblages. In these forests, establishment of terricol species is only possible on bare soil surfaces next to the trunks, on forest paths and on new surfaces created by uprooting. Most bryophytes live on rocks and on decaying logs. Under prevailing climatic conditions (periods with low relative air humidity), beech bark does not provide favourable habitats for epiphytic species, so the presence of admixing deciduous trees with heterogeneous bark structure (maple, ash, lime) is very important. The most diverse and abundant terricol and corticol bryophyte vegetation occurs in the mixed coniferous-deciduous forests in the westernmost part of Hungary (Ódor et al. 1996). A similar tendency was observed in the boreal region, where the presence of deciduous trees also increases the biodiversity of coniferous stands (Esseen et al. 1997). Forest fire is the major form of natural disturbance in many boreal forest types (Zackrisson 1977, Wein 1993, Esseen et al. 1997, Angelstam 1998). However, in moist deciduous forests (like the montane-submontane beech forests in Hungary) gap-phase dynamics is the major type of natural disturbance (Angelstam 1996, Runkle 1985). As a result, there is a less varying supply of CWD in these deciduous forests than in fire dominated boreal forests. In addition to the importance of forest authenticity and the availability of appropriate substrates, the composition of epixyl bryophyte assemblages is also strongly affected by prevailing climatic conditions within the stand. Because of not sufficiently high and constant air humidity, mosses dominate the bryophyte vegetation found on logs in zonal forests. It is only at sites with special local climate (e.g. ravines and northern slopes), where both the total cover of bryophytes and the importance of hepatics are much greater.

To understand how traditional forest management affects bryophytes depending on dead wood, one should consider both the differences in stand structures and the population biology (e.g. dispersal, establishment, competitive ability, population growth) of the species in question (Söderström 1994, Söderström and Herben 1997). Unfortunately, data are available only for a few species (e.g. Jonsson and Söderström 1988).

Managed forests are usually different from near-natural ones since large dead trees are virtually missing. Dead wood usually occurs in the form of fine woody debris (i.e. branches, thinner trees). Its supply is periodic depending on management regime. In addition, areas where large trees occur can be far from each other, when a clear-cutting system is applied in large compartments. This landscape
scale difference is especially important in those forests where natural disturbance would create much finer scale patterns, like in central European beech forests.

Kruys and Jonsson (1999) studied the importance of fine woody debris in maintaining bryophyte diversity in managed spruce stands. They showed that at low volumes of woody debris species richness increased with the proportion of fine components, whereas at higher volumes with the proportion of coarse woody debris. These results also support the conservation value of dead wood resulting from tending. In our recently thinned stand (31B) higher dead wood volume supported the appearance of some wood inhabiting species (Lophocolea heterophylla, Brachythecium rutabulum, Rhizomnium punctatum, cf. Table 2).

Large decaying logs provide suitable colonisation sites in greater amount and for much longer time than thin branches. Fine woody debris – like dead wood resulting from thinning of young stands – occurs at regular intervals producing only thin, hence rapidly decaying material (Söderström 1988a, b, Bader et al. 1995, Kruys et al. 1999). The increased colonisation probability – provided by large long-lasting logs – is important in the survival of many rare epixylous species since they are often dispersal limited. It was shown that dispersal and frequent colonisation have greater importance than competition in shaping the structure of epixylous bryophyte assemblages (Söderström 1988c, McAlister 1995).

Habitat continuity and fragmentation are two important issues while considering the role of dead wood in maintaining bryophyte diversity. Continuous availability of dead wood – in all decay phases and size classes in close proximity – is of major importance (Söderström 1988b, Rambo and Muir 1998, Kruys et al. 1999). This condition could be easily maintained by preserving a few forest reserves, where dead wood is continuously present. However, bryophytes inhabiting dead wood, mostly hepatics, are often endangered because their local populations are often small and insecure and their dispersal capacity is supposed to be limited (e.g. Lophozia adscendens, Calypogeia suecica). So, fragmentation of the habitat they require (forest with old-growth characteristics) threatens their survival (Söderström 1990). This is especially true in central European beech forests where near-natural stands are extremely rare, and most of them, like the Kékes Forest Reserve, are usually small and isolated. Here dead wood plays an extremely important role in the preservation of epixyl bryophyte populations.

All these call for a strategy where valuable near-natural forest reserves are surrounded with a matrix of managed forest in which dead wood management is carefully designed to fulfill the demands of targeted organisms. Bryophytes are only one example of the organisms associated with decaying wood and with old natural forests. Besides the obligatory conservation of these rare and often isolated habitats, it would also be important to provide the occurrence of large decaying logs in managed stands.

Although there are considerable differences between the composition and dynamics of central European beech and boreal forests, dead wood has fundamental roles and importance in ecological processes and in sustaining different organisms (in this case epixyl bryophytes) in both regions.

Acknowledgements – The authors wish to express their thanks to László Gállhidy, Erzsebet Szurdoki, Réka Aszalós and Ilona Paszterkő who took part in the field sampling. The financial support given by grants OTKA F029762, OTKA F21300, OMFB EU-98-D10-109 is greatly acknowledged. Many thanks are due to Peter Erzberger and Beáta Papp for their help in identifying bryophytes and for criticizing the manuscript. Ed Mountford, Rienk-Jan Bijlsma, Bengt Gunnar Jonsson and Nicholas Krays made useful comments on the manuscript.

References


